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Scalability of genetic biocontrols for eradicating invasive alien mammals

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Abstract

CRISPR-based gene drives offer novel solutions for controlling invasive alien species, which could ultimately extend eradication efforts to continental scales. Gene drives for suppressing invasive alien vertebrates are now under development. Using a landscape-scale individual-based model, we present the first estimates of times to eradication for long-lived alien mammals. We show that demography and life-history traits interact to determine the scalability of gene drives for vertebrate pest eradication. Notably, optimism around eradicating smaller-bodied pests (rodents and rabbits) with gene-drive technologies does not easily translate into eradication of larger-bodied alien species (cats and foxes).

Keywords

Cat, fox, gene drive, invasive mammals, mice, rabbit, rat, spatial model

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Introduction

Alien vertebrates are some of the costliest invasive alien species worldwide (Diagne et al. 2021), directly causing species extinctions (Bellard et al. 2016) and driving profound environmental change (Pyšek et al. 2020). The risk of new invasive alien species continues to increase (Seebens et al. 2017, 2021), and is intimately linked to growth in globally expanding transportation networks, widespread rapid environmental change, and geopolitical forces - including intercontinental trade agreements. In Australia, mammals are the costliest invasive taxa; with feral cats (*Felis catus*), rodents (house mice *Mus musculus* and rats *Rattus spp.*), pigs (*Sus scrofa*), rabbits (*Oryctolagus cuniculus*), and red foxes (*Vulpes vulpes*) accounting for 95% of the total costs imposed by invasive mammals over the last 50 years (Bradshaw et al. 2021). Despite some notable successes in eradicating vertebrate invasive alien species on islands (Gregory et al. 2014), continental eradications remain elusive, and are greatly hampered by a lack of socio-political resourcing and will (Pluess et al. 2012). New tools are urgently needed.

CRISPR-based gene-drive approaches promise ground-breaking tools for the eradication or suppression of invasive alien species (Esvelt et al. 2014; Webber et al. 2015). By avoiding unwanted consequences to non-target organisms, genetic biocontrols offer many advantages over classical control methods such as poison baiting, trapping or hunting (Howarth 1991). There have been promising developments in laboratories using gene-drive technology in mosquitoes (Gantz et al. 2015; Kyrou et al. 2018), fruit flies (Gantz and Bier 2015; Champer et al. 2020), mice (Grunwald et al. 2019; Weitzel et al. 2021), and proof of principle for CRISPR gene editing has been demonstrated in cats (Brackett et al. 2022). Despite great interest in developing the technology for a range of vertebrate pests (Prowse et al. 2017; Moro et al. 2018; Prowse et al. 2018; Faber et al. 2021), the feasibility of achieving large-scale eradications of these species using gene drives has not been evaluated theoretically.

Here, we investigated how differences in the life-history traits of five invasive mammals (mice, rats, rabbits, feral cats, and red foxes) interact and influence the feasibility of deploying gene-drive technologies for population suppression at large spatial scales. We used an individual-based, spatially explicit, stochastic model that provides realistic estimates of eradication probabilities and expected times to eradication, due to its ability to model large population sizes at a landscape level (see Suppl. material 1: Tables S1, S2; Birand et al. 2022). We explored the effectiveness of a Y-chromosome-linked X-chromosome-shredding drive ("driving-Y"), which targets the X-chromosome for deletion during spermatogenesis with slightly imperfect efficiency (Fig. 1A). Population suppression is achieved by producing disproportionately more male offspring, and thus limiting female numbers. Theoretical models suggest that a driving-Y strategy could be effective for population eradication (Hamilton 1967; Deredec et al. 2008, 2011; Beaghton et al. 2016; Eckhoff et al. 2017; Prowse et al. 2019; Faber et al. 2021; Birand et al. 2022), and proof-of-concept for X chromosome shredding has been demonstrated in mouse zygotes (Zuo et al. 2017). We also modelled a CRISPR homing drive (see Suppl. material 1: Tables S1, S2) targeting female fertility that is predicted to be similarly effective (Prowse et

al. 2017; Birand et al. 2022), but may be challenging to generate (Grunwald et al. 2019; Pfitzner et al. 2020; Weitzel et al. 2021). Our motivation is to explore how species-specific life history and demographic traits influence eradication probabilities and times to eradication, rather than to evaluate the efficiencies of different gene-drive strategies *per se*, which is discussed extensively elsewhere (Champer et al. 2017; Unckless et al. 2017).

Based on density estimates in Australia (*d* in Table 1), we calculated the area (*A*) that each species would occupy, assuming a population size of roughly 200,000 individuals. We then modelled the required area for each species—from 40 km^2 for mice to 100,000 km^2 for cats and foxes—as a 64 × 64 grid of patches. We used historical (or experimental) invasion records to estimate the maximum distances (Δ_i) that each species could disperse per breeding cycle. These distance estimates provide reliable representation of the distance each species would cover when the population density is low at the later stages of a successful suppression (Birand et al. 2022). A dispersal function was developed for each species that was both distance and negative density dependent, mimicking the fact that individuals would move long distances to find mates when densities are low (Diffendorfer 1998; Travis and French 2000; Matthysen 2005; Birand et al. 2022).

Results and discussions

We initially simulated various spatial gene-drive release strategies and compared the simulated times to eradication for mice (Fig. 1B, C) to find an optimal release strategy that is fast, spatially expansive, but also conservative in terms of the laboratory effort required to produce gene-drive carrying individuals for release into the wild. The number of individuals released influenced the simulated time to eradication more than the spatial release strategy used. For example, releasing 4 gene-drive carrying individuals to 16 evenly-spaced patches had the same effect as releasing 1 individual to 64 evenly-spaced patches, except when the total number of individuals released was very low (less than 16, Fig. 1B), or when the dispersal distances were small (Fig. 1C). For the remainder of our study, we assumed an achievable release size of 256 individuals released into 256 evenly-spaced patches (i.e., one individual released per patch).

In order to capture the uncertainty in some of the demographic and dispersal parameters in our simulations, we generated uniform distributions based on the parameter ranges of the probabilities of survival (ω) and polyandry (p_m), and for dispersal distances (*D*) (Table 1, also see Suppl. material 1: Tables S1, S2). We used these distributions to generate 1, 000 unique parameter combinations for each species using Latin hypercube sampling (randomLHS, R package *lhs*, Carnell 2020). We ran one simulation for each parameter combination for 500 breeding cycles (Prowse et al. 2016), and calculated the times to eradication in years based on the estimates of number of breeding cycles (n_c) in a year for each species.

The probability of eradication for small-bodied species (0.97, 1.0, 1.0, respectively for mice, rats, and rabbits) was higher than for large-bodied species (0.50, and 0.89 respectively for cats and foxes, Fig. 1D). The probabilities were lower with the homing

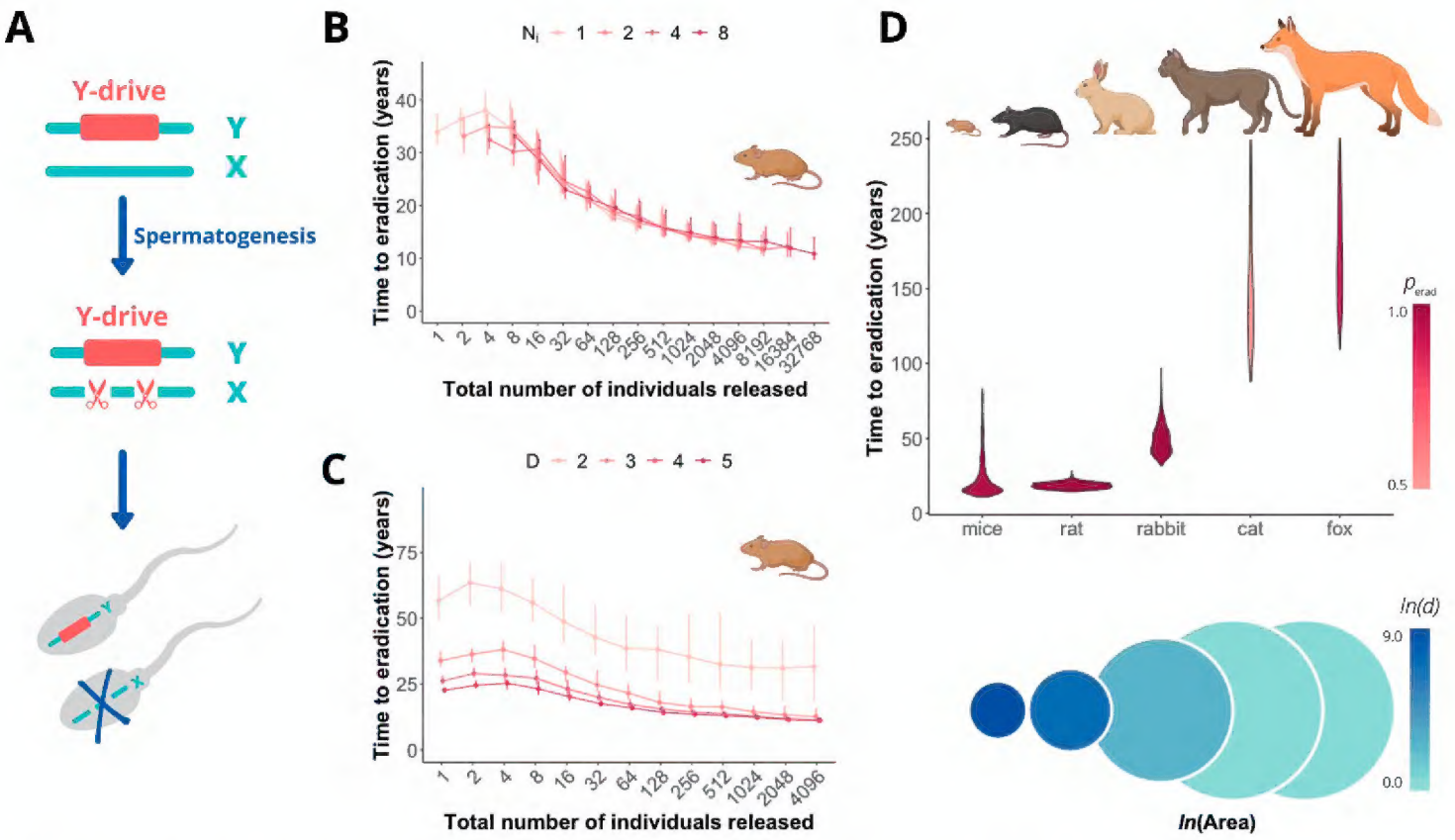

Figure 1. Times to eradication with various release strategies in mice and other invasive mammals using Y-drive. **A** the X-chromosome shredding Y-drive is located on the Y chromosome, and cuts the X chromosome at multiple locations during spermatogenesis (with probability $p_x = 0.96$). The X-bearing sperm are destroyed and eggs are predominantly fertilized by Y-bearing sperm, causing disproportionately more male offspring **B** interquartile ranges for the time to eradication of mice with various spatial release strategies when the number of individuals released per patch, N_i, is varied and the maximum dispersal distance $D = 3$ patches, and **C** when $N_i = 1$ and D is varied (100 simulations for each combination) **D** violin plots showing the distributions of simulated times to eradication (1000 simulations for each species) and circles representing areas that each species with roughly 200,000 individuals would occupy. The colors of violin plots and circles represent probabilities of eradication and density estimates, respectively.

Table 1. Parameters that are related to the demography and life-history traits for each species, along with the areas that the species are assumed to occupy with roughly 200,000 individuals, based on density estimates obtained from literature. We note that these density estimates are used for area (A) calculation only, and due to the stochastic nature of the simulations, densities change through time and also across simulations.

Species	b	n_c	age_m	ω	p_m	d	A	Δ_i	D
Mouse	6	6	2	[0.48, 0.58]	[0.41, 0.51]	5000	40	0.4	[2, 4]
Black rat	4	6	2	[0.62, 0.67]	[0.63, 0.73]	1000	200	2	[7, 9]
Rabbit	4	4	3	[0.82, 0.87]	[0.15, 0.25]	25	8000	12.5	[7, 9]
Cat	4	2	5	[0.85, 0.90]	[0.20,0.30]	2	100000	25	[3, 5]
Fox	4	2	5	[0.88, 0.93]	[0.71, 0.81]	2	100000	45	[7, 9]

b: average number of offspring per breeding cycle; n_c: number of breeding cycles in a year; age_m: maximum age (years); ω: probability of survival to the next breeding cycle; p_m: probability of multiple mating; d: density (km^{-2}); A: area (km^2); Δ_i: invasion distance per breeding cycle (km); D: corresponding distances (number of patches) in the model.
References: Brothers et al. (1985); Williams (1996); Bowen and Read (1999); Say et al. (1999); Read and Bowen (2001); Abbott (2002); Devillard et al. (2003); Baker et al. (2004); Mutze (2009); Russell (2012); Cox et al. (2013); King et al. (2014); Shiels et al. (2014); Elliott et al. (2015); Harper and Bunbury (2015); Legge et al. (2017); Barnett et al. (2018); Moro et al. (2018); Fairfax (2019); Porteus et al. (2019); Murphy and Nathan (2021).

drive than with the Y-drive (0.88, 0.90,0.91, 0.57, and 0.87; for mice, rat, rabbit, cat, and fox, respectively) due to efficient DNA repair mechanisms resulting in the evolution of functionally resistant alleles. Based on sensitivity analysis results across all species, survival (ω) had the highest influence (50.45%) on the simulated eradication probabilities with the Y-drive, followed by dispersal (46.71%) and probability of polyandry (2.83%) (Suppl. material 1: Table S1). Cats had the lowest eradication probability, and also had low dispersal (*D*) in the model (the relative influence of dispersal in probability of eradication in cats increased to 73.10%, Suppl. material 1: Table S1). Polyandry had higher influence in simulated times to eradication (28.95%), in which the relative influence of dispersal was reduced to 26.69%, and survival remained at similar levels (44.35%). We expect that polyandry might have a higher impact on eradication probabilities if the competitive ability of sperm from gene-drive carriers is reduced further than has been assumed here (Manser et al. 2020; Birand et al. 2022).

Median eradication times of roughly 200,000 individuals with the X-chromosome shredding drive were 17.7 years for mice, 18.5 years for rats, 48.0 years for rabbits, 142.3 years for cats, and 169.0 years for foxes, with nearly 90% population suppression achieved at half that time (Suppl. material 1: Table S2) (median times to eradication with the homing drive: 13.2, 14.3, 40.8, 121.5, and 110.5 years in the same species order). Simulated eradication times were much longer and also more uncertain in cats and foxes; in comparison to the shorter-lived species tested (Fig. 1D). Shorter dispersal distances resulted in longer times to eradication (e.g. Fig. 1C) mostly due to the emergence of "chase dynamics" where successive waves of local extinction and re-colonization by wild types prolonged the eradication attempt (Champer et al. 2021; Birand et al. 2022). In fact, the effect of dispersal in simulated times to eradication can override the effect of survival, and its relative influence in the time to eradication increase in species with low dispersal (Suppl. material 1: Table S1). For example, estimated eradication times for mice were more uncertain than those for rats (Fig. 1D). This is because, although mice have faster life histories than rats, they also have lower dispersal abilities so chase dynamics are more likely to arise. Similarly, lower dispersal in cats resulted in higher uncertainty in estimated eradication times compared to foxes. The relative influence of polyandry on simulated times to eradication also increased in species with high polyandry rates (Suppl. material 1: Table S1). It is certain that reliable estimates of the time to eradication will rely on a thorough understanding of movement and mating behaviors, particularly at low densities when gene drives begin to take effect.

Conclusion

Our results are in agreement with theoretical models suggesting that gene drives could eradicate large populations of short-lived mammals successfully, within reasonable time periods, and could be an attractive alternative to current lethal control methods (Prowse et al. 2017, 2018; Prowse et al. 2019; Champer et al. 2021; Birand et al. 2022). In contrast, delayed eradication times for large and long-lived species could

render gene drives less attractive as control tools for such species. However, due to their lower densities, even if time to eradication using gene drives is high, control of long-lived species is potentially possible over very large areas.

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References

Abbott I (2002) Origin and spread of the cat, *Felis catus*, on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. Wildlife Research 29(1): 51–74. https://doi.org/10.1071/WR01011

Baker P, Funk S, Bruford M, Harris S (2004) Polygynandry in a red fox population: Implications for the evolution of group living in canids? Behavioral Ecology 15(5): 766–778. https://doi.org/10.1093/beheco/arh077

Barnett LK, Prowse TAA, Peacock DE, Mutze GJ, Sinclair RG, Kovaliski J, Cooke BD, Bradshaw CJA (2018) Previous exposure to myxoma virus reduces survival of European rabbits during outbreaks of rabbit haemorrhagic disease. Journal of Applied Ecology 55(6): 2954–2962. https://doi.org/10.1111/1365-2664.13187

Beaghton A, Beaghton PJ, Burt A (2016) Gene drive through a landscape: Reaction-diffusion models of population suppression and elimination by a sex ratio distorter. Theoretical Population Biology 108: 51–69. https://doi.org/10.1016/j.tpb.2015.11.005

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. Biology Letters 12(2): e20150623. https://doi.org/10.1098/rsbl.2015.0623

Birand A, Cassey P, Ross JV, Russell JC, Thomas PQ, Prowse TAA (2022) Gene drives for vertebrate pest control: Realistic spatial modelling of eradication probabilities and times for island mouse populations. Molecular Ecology 31(6): 1907–1923. https://doi.org/10.1111/mec.16361

Bowen Z, Read J (1999) Population and demographic patterns of rabbits (*Oryctolagus cuniculus*) at Roxby Downs in arid South Australia and the influence of rabbit haemorrhagic disease. Wildlife Research 25(6): 655–662. https://doi.org/10.1071/WR98004

Brackett NF, Davis BW, Adli M, Pomés A, Chapman MD (2022) Evolutionary biology and gene editing of cat allergen, fel d 1. The CRISPR Journal 5(2): 213–223. https://doi.org/10.1089/crispr.2021.0101

Bradshaw CJA, Hoskins AJ, Haubrock PJ, Cuthbert RN, Diagne C, Leroy B, Andrews L, Page B, Cassey P, Sheppard AW, Courchamp F (2021) Detailed assessment of the reported economic costs of invasive species in Australia. NeoBiota 67: 511–550. https://doi.org/10.3897/neobiota.67.58834

Brothers N, Skira I, Copson G (1985) Biology of the feral cat, *Felis catus* (L.), on Macquarie Island. Wildlife Research 12(3): 425–436. https://doi.org/10.1071/WR9850425

Carnell R (2020) lhs: Latin Hypercube Samples. https://CRAN.R-project.org/package=lhs

Champer J, Reeves R, Oh SY, Liu C, Liu J, Clark AG, Messer PW (2017) Novel CRISPR/Cas9 gene drive constructs reveal insights into mechanisms of resistance allele formation and drive efficiency in genetically diverse populations. PLoS Genetics 13(7): 1–18. https://doi.org/10.1371/journal.pgen.1006796

Champer J, Yang E, Lee E, Liu J, Clark AG, Messer PW (2020) A CRISPR homing gene drive targeting a haplolethal gene removes resistance alleles and successfully spreads through a cage population. Proceedings of the National Academy of Sciences of the United States of America 117(39): 24377–24383. https://doi.org/10.1073/pnas.2004373117

Champer J, Kim IK, Champer SE, Clark AG, Messer PW (2021) Suppression gene drive in continuous space can result in unstable persistence of both drive and wild-type alleles. Molecular Ecology 30(4): 1086–1101. https://doi.org/10.1111/mec.15788

Cox T, Strive T, Mutze G, West P, Saunders G (2013) Benefits of rabbit biocontrol in Australia, PestSmart Toolkit publication, Technical report, Invasive Animals Cooperative Research Centre, Canberra.

Deredec A, Burt A, Godfray HCJ (2008) The population genetics of using homing endonuclease genes in vector and pest management. Genetics 179(4): 2013–2026. https://doi.org/10.1534/genetics.108.089037

Deredec A, Godfray HCJ, Burt A (2011) Requirements for effective malaria control with homing endonuclease genes. Proceedings of the National Academy of Sciences of the United States of America 108(43): E874–E880. https://doi.org/10.1073/pnas.1110717108

Devillard S, Say L, Pontier D (2003) Dispersal pattern of domestic cats (*Felis catus*) in a promiscuous urban population: Do females disperse or die? Journal of Animal Ecology 72(2): 203–211. https://doi.org/10.1046/j.1365-2656.2003.00692.x

Diagne C, Leroy B, Vaissiére AC, Gozlan RE, Roiz D, Jarić I, Salles JM, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature 592(7855): 571–576. https://doi.org/10.1038/s41586-021-03405-6

Diffendorfer JE (1998) Testing models of source-sink dynamics and balanced dispersal. Oikos 81(3): 417–433. https://doi.org/10.2307/3546763

Eckhoff PA, Wenger EA, Godfray HCJ, Burt A (2017) Impact of mosquito gene drive on malaria elimination in a computational model with explicit spatial and temporal dynamics. Proceedings of the National Academy of Sciences of the United States of America 114(2): E255–E264. https://doi.org/10.1073/pnas.1611064114

Elliott G, Greene T, Nathan H, Russell JC (2015), Winter bait uptake trials and related field work on Antipodes Island in preparation for mouse (*Mus musculus*) eradication. Technical

report, DOC Research and Development Series 345, Department of Conservation, New Zealand.

Esvelt KM, Smidler AL, Catteruccia F, Church GM (2014) Emerging technology: Concerning RNA-guided gene drives for the alteration of wild populations. eLife 3: e03401. https://doi.org/10.7554/eLife.03401

Faber NR, McFarlane GR, Gaynor RC, Pocrnic I, Whitelaw CBA, Gorjanc G (2021) Novel combination of CRISPR-based gene drives eliminates resistance and localises spread. Scientific Reports 11(1): e3719. https://doi.org/10.1038/s41598-021-83239-4

Fairfax RJ (2019) Dispersal of the introduced red fox (*Vulpes vulpes*) across Australia. Biological Invasions 21(4): 1259–1268. https://doi.org/10.1007/s10530-018-1897-7

Gantz VM, Bier E (2015) The mutagenic chain reaction: A method for converting heterozygous to homozygous mutations. Science 348(6233): 442–444. https://doi.org/10.1126/science.aaa5945

Gantz VM, Jasinskiene N, Tatarenkova O, Fazekas A, Macias VM, Bier E, James AA (2015) Highly efficient Cas9-mediated gene drive for population modification of the malaria vector mosquito *Anopheles stephensi*. Proceedings of the National Academy of Sciences of the United States of America 112(49): E6736–E6743. https://doi.org/10.1073/pnas.1521077112

Gregory SD, Henderson W, Smee E, Cassey P (2014) Eradications of vertebrate pests in Australia: A review and guidelines for future best practice. Technical report, Invasive Animals CRC, Canberra.

Grunwald HA, Gantz VM, Poplawski G, Xu X-RS, Bier E, Cooper KL (2019) Super-Mendelian inheritance mediated by CRISPR-Cas9 in the female mouse germline. Nature 566(7742): 105–109. https://doi.org/10.1038/s41586-019-0875-2

Hamilton WD (1967) Extraordinary sex ratios. Science 156(3774): 477–488. https://doi.org/10.1126/science.156.3774.477

Harper GA, Bunbury N (2015) Invasive rats on tropical islands: Their population biology and impacts on native species. Global Ecology and Conservation 3: 607–627. https://doi.org/10.1016/j.gecco.2015.02.010

Howarth FG (1991) Environmental impacts of classical biological control. Annual Review of Entomology 36(1): 485–509. https://doi.org/10.1146/annurev.en.36.010191.002413

King C, Winstanley T, Innes J, Gleeson D (2014) Multiple paternity and differential male breeding success in wild ship rats (*Rattus rattus*). New Zealand Journal of Ecology 38(1): 76–85.

Kyrou K, Hammond AM, Galizi R, Kranjc N, Burt A, Beaghton AK, Nolan T, Crisanti A (2018) A CRISPR–Cas9 gene drive targeting *doublesex* causes complete population suppression in caged *Anopheles gambiae* mosquitoes. Nature Biotechnology 36(11): 1062–1066. https://doi.org/10.1038/nbt.4245

Legge S, Murphy B, McGregor H, Woinarski J, Augusteyn J, Ballard G, Baseler M, Buckmaster T, Dickman C, Doherty T, Edwards G, Eyre T, Fancourt B, Ferguson D, Forsyth D, Geary W, Gentle M, Gillespie G, Greenwood L, Hohnen R, Hume S, Johnson C, Maxwell M, McDonald P, Morris K, Moseby K, Newsome T, Nimmo D, Paltridge R, Ramsey D, Read J, Rendall A, Rich M, Ritchie E, Rowland J, Short J, Stokeld D, Sutherland D, Wayne A, Woodford L, Zewe F (2017) Enumerating a continental-scale threat: How many feral

cats are in Australia? Biological Conservation 206: 293–303. https://doi.org/10.1016/j.biocon.2016.11.032

Manser A, König B, Lindholm AK (2020) Polyandry blocks gene drive in a wild house mouse population. Nature Communications 11(1): e5590. https://doi.org/10.1038/s41467-020-18967-8

Matthysen E (2005) Density-dependent dispersal in birds and mammals. Ecography 28(3): 403–416. https://doi.org/10.1111/j.0906-7590.2005.04073.x

Moro D, Byrne M, Kennedy M, Campbell S, Tizard M (2018) Identifying knowledge gaps for gene drive research to control invasive animal species: The next CRISPR step. Global Ecology and Conservation 13: e00363. https://doi.org/10.1016/j.gecco.2017.e00363

Murphy EC, Nathan HW (2021) *Mus muculus*. In: King CM, Forsyth DM (Eds) The handbook of New Zealand mammals. 3rd edn., CSIRO Publishing, Melbourne, 161–240.

Mutze GJ (2009) Changes in body condition and body size affect breeding and recruitment in fluctuating house mouse populations in south-eastern Australia. Austral Ecology 34(3): 278–293. https://doi.org/10.1111/j.1442-9993.2008.01929.x

Pfitzner C, White MA, Piltz SG, Scherer M, Adikusuma F, Hughes JN, Thomas PQ (2020) Progress toward zygotic and germline gene drives in mice. The CRISPR Journal 3(5): 388–397. https://doi.org/10.1089/crispr.2020.0050

Pluess T, Cannon R, Jarošík V, Pergl J, Pyšek P, Bacher S (2012) When are eradication campaigns successful? A test of common assumptions. Biological Invasions 14(7): 1365–1378. https://doi.org/10.1007/s10530-011-0160-2

Porteus TA, Reynolds JC, McAllister MK (2019) Population dynamics of foxes during restricted-area culling in Britain: Advancing understanding through state-space modelling of culling records. PLoS ONE 14(11): e0225201. https://doi.org/10.1371/journal.pone.0225201

Prowse TAA, Bradshaw CJA, Delean S, Cassey P, Lacy RC, Wells K, Aiello-Lammens ME, Akçakaya HR, Brook BW (2016) An efficient protocol for the global sensitivity analysis of stochastic ecological models. Ecosphere 7(3): e01238. https://doi.org/10.1002/ecs2.1238

Prowse TAA, Cassey P, Ross JV, Pfitzner C, Wittmann TA, Thomas P (2017) Dodging silver bullets: good CRISPR gene-drive design is critical for eradicating exotic vertebrates. Proceedings of the Royal Society B: Biological Sciences 284(1860): e20170799. https://doi.org/10.1098/rspb.2017.0799

Prowse TAA, Cassey P, Ross JV, Pfitzner C, Wittmann T, Thomas P (2018) Correction to 'Dodging silver bullets: good CRISPR gene-drive design is critical for eradicating exotic vertebrates'. Proceedings of the Royal Society B: Biological Sciences 285(1888): e20182048. https://doi.org/10.1098/rspb.2018.2048

Prowse TAA, Adikusuma F, Cassey P, Thomas P, Ross JV (2019) A Y-chromosome shredding gene drive for controlling pest vertebrate populations. eLife 8: e41873. https://doi.org/10.7554/eLife.41873

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biological Reviews of the Cambridge Philosophical Society 95(6): 1511–1534. https://doi.org/10.1111/brv.12627

Read J, Bowen Z (2001) Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. Wildlife Research 28(2): 195–203. https://doi.org/10.1071/WR99065

Russell JC (2012) Spatio-temporal patterns of introduced mice and invertebrates on Antipodes Island. Polar Biology 35(8): 1187–1195. https://doi.org/10.1007/s00300-012-1165-8

Say L, Pontier D, Natoli E (1999) High variation in multiple paternity of domestic cats (*Felis catus* L.) in relation to environmental conditions. Proceedings of the Royal Society of London. Series B, Biological Sciences 266(1433): 2071–2074. https://doi.org/10.1098/rspb.1999.0889

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Stajerova K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communications 8(1): e14435. https://doi.org/10.1038/ncomms14435

Seebens H, Bacher S, Blackburn TM, Capinha C, Dawson W, Dullinger S, Genovesi P, Hulme PE, van Kleunen M, Kühn I, Jeschke JM, Lenzner B, Liebhold AM, Pattison Z, Pergl J, Pyšek P, Winter M, Essl F (2021) Projecting the continental accumulation of alien species through to 2050. Global Change Biology 27(5): 970–982. https://doi.org/10.1111/gcb.15333

Shiels AB, Pitt WC, Sugihara RT, Witmer GW (2014) Biology and impacts of Pacific Island invasive species. 11. *Rattus rattus*, the Black Rat (Rodentia: Muridae). Pacific Science 68(2): 145–184. https://doi.org/10.2984/68.2.1

Travis J, French R (2000) Dispersal functions and spatial models: Expanding our dispersal toolbox. Ecology Letters 3(3): 163–165. https://doi.org/10.1046/j.1461-0248.2000.00141.x

Unckless RL, Clark AG, Messer PW (2017) Evolution of resistance against CRISPR/Cas9 gene drive. Genetics 205(2): 827–841. https://doi.org/10.1534/genetics.116.197285

Webber BL, Raghu S, Edwards OR (2015) Opinion: Is CRISPR-based gene drive a biocontrol silver bullet or global conservation threat? Proceedings of the National Academy of Sciences of the United States of America 112(34): 10565–10567. https://doi.org/10.1073/pnas.1514258112

Weitzel AJ, Grunwald HA, Levina R, Gantz VM, Hedrick SM, Bier E, Cooper KL (2021) Meiotic Cas9 expression mediates genotype conversion in the male and female mouse germline. bioRxiv. https://doi.org/10.1101/2021.03.16.435716

Williams CK (1996) Ecological challenges to controlling wild rabbits in Australia using virally-vectored immunocontraception. Proceedings of the Seventeenth Vertebrate Pest Conference 58: 24–30.

Zuo E, Huo X, Yao X, Hu X, Sun Y, Yin J, He B, Wang X, Shi L, Ping J, Wei Y, Ying W, Wei W, Liu W, Tang C, Li Y, Hu J, Yang H (2017) CRISPR/Cas9-mediated targeted chromosome elimination. Genome Biology 18(1): e224. https://doi.org/10.1186/s13059-017-1354-4

Supplementary material 1

Tables S1, S2

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Data type: Pdf file

Explanation note: Methods.

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